doi:10.1111/j.1365-2052.2006.01487.x

QTLs associated with growth traits and abdominal fat weight and their interactions with gender and hatch in commercial meat-type chickens

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Summary

Associations between microsatellite markers and traits related to growth and fatness were investigated using resource broiler population. A sire-line × dam-line F_1 male was backcrossed to 12 dam-line females to produce 24 sires and 47 dams of the backcross 1 (BC_1) generation. These 71 parents were genotyped with 76 microsatellite markers. Following full-sib mating among the parents, 234 BC_1–F_2 progeny were phenotyped for five growth traits (body weight at 49 days from hatch, wog weight, front half weight, breast weight and tender weight) and abdominal fat weight. Maximum likelihood analysis was used to estimate the marker effects and to evaluate their statistical significance. Individual marker–trait analysis revealed 44 significant associations out of the 456 marker–trait combinations. Correction for multiple comparisons by controlling the false discovery rate (FDR) resulted in 12 significant associations at FDR = 10% with markers on chromosomes 1, 2, 5 and 13. Seventy-five percent of the 44 significant associations displayed no dependence on either hatch or gender; half of the remaining associations displayed dependence of the quantitative trait loci (QTL) effect on hatch × gender interaction. Thus, the analysed traits in this study may be dependent on external factors.

Keywords broilers, chicken, gender, hatch, interactions, maximum likelihood, quantitative trait loci.

Introduction

Several genome-wide search studies in chicken have been conducted during the last few years. Van Kaam *et al.* (1999) studied the association of markers and growth traits using 420 genetic markers and a large population size. The resource population was based on a cross between two parental lines that were previously selected for high body weight. The resulting number of detected quantitative trait loci (QTL) was very limited. Using the same population, no significant QTL affecting growth traits were found by Hamoen *et al.* (2001) following a Z-chromosome scan. Sewalem *et al.* (2002) used 101 microsatellite markers and an F_2 population resulting from a cross of a broiler sire-line and an egg-laying line in a genome-wide analysis to detect QTL affecting body weight at 3, 6 and 9 weeks with QTLs located on chromosomes 1, 2, 4, 7, 8 and 13. Carlborg *et al.* (2004) used a novel approach (simultaneous mapping of epistatic QTL) to increase power for QTL detection; they revealed clusters of QTL pairs with similar genetic effects on growth. Carlborg *et al.* (2004) and De Koning *et al.* (2004) investigated the application of QTL identified in experimental crosses of chickens to commercial populations. Following intensive selection for efficient growth in broilers for more than 50 generations, many QTL affecting these traits are still segregating.

The objective of the current study was to identify microsatellite marker loci associated with growth performance and abdominal fat deposition in chickens using a commercial broiler resource population. In addition, we tested whether the QTLs detected in this study by the maximum

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Accepted for publication 7 May 2006

likelihood (ML) approach are independent of hatch and/or of gender.

Materials and methods

Resource population

A resource population was established by the Arbor Acres Farm (AAF) poultry breeding company. A single grandsire produced from a cross between the male-line L-03 and the female-line L-14 was backcrossed with 12 randomly selected granddams of the female-line L-14. From these crosses, 353 backcross 1 (BC_1) progeny in four hatches were obtained. Seventy-one of these progeny (24 males and 47 females) were chosen randomly as the parents of the next generation. Two hundred and thirty-four BC_1–F_2 progeny from full-sib matings of the 71 parents were phenotyped for the following traits: body weight at 7 weeks of age, abdominal fat weight, wog weight (slaughtered chicken body without head and feathers), front half weight (mainly legs), breast weight and tender weight (a part of the breast that is tucked underneath the main part of the breast). Mean values and standard errors are given in Table 1. All birds were reared in the AAF facilities, fed *ad libitum*, weighed and slaughtered at 7 weeks of age. Carcass components were evaluated at the slaughterhouse.

Genotyping

Blood samples were taken from each individual of generations F_1 (13) and BC_1 (71). The 13 grandparents were genotyped with about 150 microsatellite markers of which 50% (76) were informative, with the grandsire being heterozygous and his mate having a different heterozygote genotype. The 76 informative markers were on 22 of the 39 chicken chromosomes.

The 71 parents from generation BC_1 were genotyped with the 76 informative microsatellite markers. Based on the genotype information, we determined the marker alleles that were transferred from the grandsire to his 24 sons (sires of BC_1) and to his 47 daughters (dams of BC_1).

Statistical methodology

Mean scores of progeny per genotype were transformed by scaling and centralizing the data as follows: the trait value of each phenotype x_{ij} was replaced by $(x_{ij}-m_i)/s_i$, where m_i and s_i are the mean and standard deviation values respectively of the trait in each of the four hatch–gender groups. We adopted the QTL–environment interaction model to examine the QTL interaction effects with gender (G), hatch (H) and their interaction (G × H; Jansen *et al.* 1995; Korol *et al.* 1998). In fitting the mapping model, we allowed for different m_i and s_i in the model.

Because of large map distances between most markers, we used a marker analysis instead of an interval analysis. For an arbitrary genotype *j*, the trait measurement in the *i*th environment (one of the four gender × hatch combinations) can be presented as:

$$x_{ij} = \mu_i + 0.5ga_i + e_{ij}, \quad (1)$$

where μ_i is the mean trait value in the *i*th environment, g is either +1 (for q_1 genotypes) or −1 (for q_2 genotypes), a_i is the effect of allele substitution at putative QTL on trait in environment *i*, and e_i is a random variable with zero mean and variance σ_i^2. If we find that $a_i\sigma$ for any *i*, then no G × E interaction is manifested by q_1/q_2. Model (1) was used to analyse our data based on the ML procedure implemented in MultiQTL (http://www.multiqtl.com).

In cases where the QTL effect depended on gender [male (m) vs. female (f)], hatch [hatch 1 (h_1) vs. hatch 2 (h_2)] or their interaction, one may reduce the QTL detection power by ignoring this dependence. Therefore, our analysis included the general case assuming that the QTL effect may vary among the four groups: h_1f, h_1m, h_2f and h_2m. The next step was testing submodels for the dependence of QTLs on hatch, on gender or on the interaction between them: (1) $h_1 \neq h_2$ & m = f; (2) $h_1 = h_2$ & m ≠ f; (3) $h_1 \neq h_2$ & m ≠ f and (4) $h_1 = h_2$ & m = f. A log-likelihood ratio of one of the first three hypotheses to that of the fourth allows testing the significance of the corresponding interaction (QTL × hatch, QTL × gender or QTL × hatch × gender).

After significance testing of the main effects and the foregoing interactions for each marker–trait combination, the experiment-wise level of significance was calculated using the false discovery rate (FDR) approach developed by Benjamini & Hochberg (1995).

Results

Significant marker–trait associations

Markers in this study were distantly distributed relative to each other, with an average interval of 50 cM. Therefore, it was not possible to use an interval mapping approach, and the data were analysed using single marker–trait associations. For each progeny group, i.e. sires (S), dams (D), or dams + sires (D + S), we analysed 76 markers for each of the six traits. Thus, the number of individual tests H_1 vs. H_0 (presence vs. absence of association) were 456 (76 markers × 6 traits). The significance of deviation from H_0 was performed by a permutation test for each marker–trait combination. Significant markers were chosen following ML analysis using one of three tests: S, D or D + S (Table 1). The total number of significant marker–trait associations ($P < 0.05$) was 44, including 17 significant H_1 cases for sires, 17 for dams and 10 for dams and sires. In 33 cases (75%), the effect of the QTL on the trait was independent of the gender, hatch or the interaction between them

Table 1 Significant marker–trait associations without adjustment for multiple comparisons.

Trait[1]	Marker	Chromosome	Position	Model (n)[2]	Submodel[3]	d/σ[4]	P-value[5]	Number of permutations
Body weight, M = 2267 g, SE = 34.6	*ADL0037*	1	319	D (44)	4	−0.56/0.95	0.0072	10 000
	MCW0102	1	394	D + S (65)	1	−0.09; −0.8/0.95	0.0011	1000
	MCW0088	2	274	D + S (64)	3a	0.14; 0.93/0.96	0.023	1000
	ADL0225	13	2	D (41)	4	−0.51/0.95	0.016	1000
Wog weight, M = 1546 g, SE = 28.3	*ADL0019*	1	122	D (38)	3a	0.15; 1.17/0.98	0.015	1000
	MCW0102	1	394	S (23)	4	−0.98/0.89	0.0001	10 000
	MCW0088	2	274	D + S (64)	4	0.38/0.92	0.009	1000
	ADL0187	5	96	D + S (69)	4	−0.34/0.98	0.025	1000
	ADL0225	13	2	D (41)	4	−0.57/0.92	0.016	1000
Front half weight, M = 807 g, SE = 14.6	*MCW0102*	1	394	S (23)	4	−0.95/0.89	0.0001	10 000
	ADL0152	2	64	D (40)	4	0.48/0.94	0.044	1000
	MCW088	2	274	D + S (64)	4	0.46/0.93	0.0019	10 000
	HUJ0006	3	89	S (18)	1	−0.74/0.69; −0.70/0.94	0.029	1000
	ADL0327	3	182	D (45)	3b	−0.93; 0.05/0.97	0.005	1000
	ADL0237	3	275	S (18)	4	0.72/0.88	0.024	1000
	ADL0211	9	28	D (24)	4	0.76/0.93	0.01	1000
	ADL0225	13	2	D (41)	4	−0.66/0.91	0.0013	10 000
	ADL0310	13	23	S (19)	4	0.69/0.90	0.028	1000
Tender weight, M = 72.1 g, SE = 1.5	*UMA0353*	1	310	D + S (45)	4	0.60/0.94	0.0019	10 000
	MCW0102	1	394	S (23)	4	−0.95/0.89	0.0051	1000
	ADL0198	1	435	S (17)*	4	−0.89/0.82	0.005	1000
	MCW0145	1	455	D (44)	4	0.51/0.91	0.015	1000
	ADL0152	2	64	D (40)	4	0.56/0.92	0.0042	10 000
	ADL0217	2	121	D (42)	4	0.62/0.88	0.0012	10 000
	MCW0088	2	274	D + S (64)	1	0.12; 0.74/0.94	0.022	1000
	ADL0237	3	275	S (18)	4	0.82/0.85	0.0034	10 000
	ADL0225	13	2	D (41)	1	−0.37;−1.1/0.90	0.0008	10 000
Breast weight, M = 290 g, SE = 5.4	*MCW0102*	1	394	S (23)	4	−0.95/0.89	0.0006	10 000
	MCW0145	1	455	D (44)	4	0.51/0.96	0.013	1000
	ADL0217	2	121	D (42)	4	0.56/0.88	0.0061	10 000
	MCW0088	2	274	D (45)	4	0.54/0.95	0.0063	10 000
	ADL0237	3	275	S (18)	4	0.72/0.88	0.014	1000
	ADL0225	13	2	D (41)	4	−0.66/0.93	0.0009	10 000
Abdominal fat weight, M = 38.7 g, SE = 1.3	*ADL0150*	1	173	S (17)	4	0.93/0.94	0.0012	10 000
	MCW0109	1	320	S (23)	3b	1.37; 0.21/0.89	0.015	1000
	MCW0088	2	274	S (19)	4	0.80/0.86	0.0039	10 000
	ADL0146	2	403	S (23)	4	−0.59/0.91	0.013	1000
	LEI0166	3	300	D + S (42)*	2	−0.87; 0.25/0.92	0.0048	10 000

Table 1 Continued

Trait[1]	Marker	Chromosome	Position	Model (n)[2]	Submodel[3]	d/σ^4	P-value[5]	Number of permutations
	ADL0143	4	0	D + S (70)	4	0.44/0.97	0.007	1000
	ADL0166	5	162	S (24)	3c	1.32; −0.31/0.90	0.001	1000
	ADL0326	7	142	S (19)	4	0.6/0.88	0.027	1000
	ADL0272	10	37	S (22)	3a	0.82;−0.46/0.88	0.032	2000
	ADL0372	12	0	D + S (50)*	4	−0.53/0.95	0.007	1000
	ADL0273	Z	73	D (47)	4	−0.53/0.95	0.013	1000

[1]Mean values (M) and standard errors (SE) are given across hatches and genders.
[2]D, dams; S, sires; D + S, dams + sires; n, number of subjects in each analysis.
[3]Submodels with h = hatch, m = male, f = female effects: (1) $h_1 \neq h_2$ & m = f; (2) $h_1 = h_2$ & m ≠ f; (3) $h_1 \neq h_2$ & m ≠ f [(a) $(h_1f = h_1m = h_2m) \neq h_2f$; (b) $h_1f \neq (h_1m = h_2f = h_2m)$; (c) $h_1m \neq (h_1f = h_2f = h_2m)$] and (4) $h_1 = h_2$ & m = f.
[4](d/σ), QTL substitution effect and residual standard variation (if any of the models 1–3 are indicated, corresponding parameters are shown in the order defined by the model).
[5]P-value is significance of QTL effects as a deviation using a permutation test.
*Significant deviation from the expected 1:1 segregation at the marker locus.

(submodel 4). In four cases (9.1%), interactions between the QTL and hatch were found (submodel 1), and an interaction was found in one case (2.3%) between QTLs and gender (submodel 2). The three-way interaction, i.e. QTL × hatch × gender (submodel 3) was found in six cases (13.6%; Table 1). In total, 26 significant markers were detected; some of them were in association with more than one trait (Table 2).

The marker *MCW0088* (chromosome 2 at position 274 cM) was significantly associated with all five growth traits, as well as with abdominal fat weight. Two other markers (*MCW0102* and *ADL0225*) were significantly associated with the five growth traits, while *ADL0237* was associated with three of them (front half, breast weight and tender weight). The six markers that were significantly associated with breast weight were also significantly associated with tender weight. Among traits, abdominal fat weight had the most associations (11), followed by tender and half weight (nine), breast weight (six), wog weight (five) and body weight (four).

Using the results of the individual trait–marker tests that were declared significant, we calculated the total number of significant cases using FDR analysis. The correction for multiple comparisons was conducted at the 5% and 10% levels of FDR (Table 3). We obtained two significant effects at the 0.05 level and 12 effects at the 0.1 level (Table 3). These 12 effects were associated with only six marker loci on chromosomes 1, 2, 5 and 13; *MCW0102* was significant four times, *ADL0225* three times and four markers were significant once each.

The sire-average model had the best power in the FDR approach (5%), where two associations were detected at very high significance (0.0001). At lower FDR stringency (10%), the difference between the models decreased so that each of the three models (S, D and D + S) has detected approximately the same number of significant effects (five cases for S, four for D and three for D + S). Among these 12 cases, the most frequent was submodel (4), which assumes no interaction between the QTL effect and gender, hatch or the interaction gender × hatch.

Dependence of QTL effects on gender and hatch

No interaction between gender and hatch was found for the six traits. We adopted the approach for analysis of a QTL × 'environment' interaction (Jansen *et al.* 1995; Korol *et al.* 1998) by considering hatch and gender as environments for the QTL effects. The results of the analysis are shown in Table 4.

Significant deviations from model 4 assuming $h_1 = h_2$ & m = f (no dependence of QTL effect on gender, hatch or interaction between them) were detected in 11 of 44 possible cases. Among these 11 cases, four were $\{h_1 \neq h_2, m = f\}$, and one was $\{h_1 = h_2, m \neq f\}$. The remaining were submodels of the model $\{h_1 \neq h_2, m \neq f\}$: three

Table 2 Significant associations between 26 microsatellite markers and the six traits[1] measured in chickens.

Chromosome	Position	Marker	BW	WW	FH	TW	BrW	AF	Total
1	122	*ADL0019*		X					1
1	173	*ADL0150*						X	1
1	310	*UMA0353*				X			1
1	319	*ADL0037*	X						1
1	320	*MCW0109*						X	1
1	394	*MCW0102*	X	X	X	X	X		5
1	435	*ADL0198*				X			1
1	455	*MCW0145*				X	X		2
2	64	*ADL0152*			X	X			2
2	121	*ADL0217*				X	X		2
2	274	*MCW0088*	X	X	X	X	X	X	6
2	403	*ADL0146*						X	1
3	89	*HUJ0006*			X				1
3	182	*ADL0327*			X				1
3	275	*ADL0237*			X	X	X		3
3	300	*LEI0166*						X	1
4	0	*ADL0143*						X	1
5	96	*ADL0187*						X	1
5	162	*ADL0166*		X					1
7	142	*ADL0326*						X	1
9	28	*ADL0211*			X				1
10	37	*ADL0272*						X	1
12	0	*ADL0372*						X	1
13	2	*ADL0225*	X	X	X	X	X		5
13	23	*ADL0310*			X				1
Z	73	*ADL0273*						X	1
Total		26	4	5	9	9	6	11	44

[1]Trait abbreviations are BW, body weight at 7 weeks; WW, wog weight; FH, front half weight; TW, tender weight; BrW, breast weight; AF, abdominal fat weight.

Table 3 Significant QTL effects allowing for QTL–environmental interaction, based on the false discovery rate (FDR) analysis.

Model (S, D, D + S)	FDR (total significance; %)	Trait[1]	Marker	Chromosome	Result (best submodel)[2]	*P*-value (number of permutations)
S (23)	5	WW	*MCW0102*	1	4	0.0001 (10 000)
S (23)	''	FH	*MCW0102*	1	4	0.0001 (10 000)
S (23)	10	WW	*MCW0102*	1	4	0.0001 (10 000)
S (23)	''	FH	*MCW0102*	1	4	0.0001 (10 000)
S (23)	''	BrW	*MCW0102*	1	4	0.0006 (10 000)
S (17)	''	AF	*ADL0150*	1	4	0.0012 (10 000)
S (24)	''	AF	*ADL0166*	5	3c	0.0010 (10 000)
D (41)	''	FH	*ADL0225*	13	4	0.0013 (10 000)
D (41)	''	TW	*ADL0225*	13	1	0.0008 (10 000)
D (42)	''	TW	*ADL0217*	2	4	0.0012 (10 000)
D (41)	''	BrW	*ADL0225*	13	4	0.0009 (10 000)
D + S (65)	''	BW	*MCW0102*	1	1	0.0011 (10 000)
D + S (64)	''	FH	*MCW0088*	2	4	0.0019 (10 000)
D + S (45)	''	TW	*UMA0353*	1	4	0.0019 (10 000)

[1]Trait abbreviations are BW, body weight at 7 weeks; WW, wog weight; FH, front half weight; TW, tender weight; BrW, breast weight; AF, abdominal fat.
[2]For submodel designations see Table 1.

Table 4 Interactions between QTL and either hatch or gender.

Trait[1]	Marker	Chromosome	Model (*n*)[2]	Result (submodel)	*P*-value (number of permutations)
BW	*MCW0102*	1	D + S (65)	1	0.0011 (1000)
	MCW0088	2	D + S (64)	3a	0.023 (1000)
WW	*ADL0019*	1	D (38)	3a	0.015 (1000)
FH	*HUJ0006*	3	S (18)	1	0.029 (1000)
	ADL0327	3	D (45)	3b	0.005 (1000)
TW	*MCW0088*	2	D + S (64)	1	0.022 (1000)
	ADL0225	13	D (41)	1	0.0008 (10 000)
AF	*MCW0109*	1	S (23)	3b	0.015 (1000)
	LEI0166	3	D + S (42)	2	0.0048 (10 000)
	ADL0166	5	S (24)	3c	0.001 (1000)
	ADL0272	10	S (22)	3a	0.032 (1000)

Here, unlike Tables 1–3, significant deviation from the hypothesis {H_0: $h_1 = h_2$, m = f} was tested assuming the existence of the QTL (i.e. H_0 means that the QTL exists but its effect does not depend on progeny's hatch or gender).

For submodel designations see Table 1.

[1]Trait abbreviations are BW, body weight at 7 weeks; WW, wog weight; FH, front half weight; TW, tender weight; AF, abdominal fat.

[2]D, dams; S, sires; D + S, dams + sires; *n*, number of subjects in each analysis.

($h_1f = h_1$, $m = h_2m$) $\neq h_2f$, two $h_1f \neq (h_1m = h_2f = h_2m)$ and one $h_1m \neq (h_1f = h_2f = h_2m)$. In other words, 45% of these QTL effects were dependent only on one of the 'environments' (gender or hatch). QTL at *MCW0102* was associated with body weight that depended on hatch only (submodel 1). Abdominal fat weight was the only trait in which the QTL effect in females was different from the QTL effect in males.

Discussion

Correction of the results based on the FDR approach reduced the number of significant results from 44 to 2 and 12 associations at 5% and 10% FDR respectively. Clearly, the FDR correction is necessary to compensate for the effect of multiple parallel tests.

Two aspects of the effect of gender and hatch had to be taken into account in the foregoing analysis. First, the trait values may display a dependence on either gender or hatch, or both. Secondly, the QTLs in question may also depend on these 'environmental' factors. If ignored, the dependence of mean trait values on either hatch or gender or hatch × gender may cause biases in the estimated QTL effects because alternative marker groups in the mapping population are unequally represented (owing to rather small sample size of genotyped individuals). A special QTL mapping model was used to deal with the second aspect. In our analysis, a QTL × E model (Jansen *et al.* 1995; Korol *et al.* 1998) was used. If the QTL effect depends on the environment and this dependence is ignored in the mapping model, the QTL detection power may be reduced and the resulting estimates are biased (Korol *et al.* 1998). In our recent analysis, only 20% of the significant trait–marker combinations (11 of 44 cases) displayed QTL × E interaction (either with hatch or gender), and in 55% of these cases, a three-way interaction was detected.

For the past several years evidence has accumulated about gender differences in amount of body fat and its distribution (Rattarasarn *et al.* 2004). Men more commonly gain fat in the intra-abdominal visceral fat depots compared with women because of differences in lipid metabolism (Williams 2004). These substantial differences may, in part, be associated with regional regulation of lipolysis and lipogenesis that mediate via α-adrenergic receptors. *In vitro* and *in vivo* data support this observation of different lipolytic sensitivity in fat depots in women compared with men. Furthermore, fatty acid uptake in some depots is as high as sevenfold in men compared with women (Williams 2004). Thus, interactions between QTL and gender might be a main factor influencing fat accumulation and distribution.

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